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Ecology and ecological genetics of seed dormancy in downy brome

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Downy brome, an obligately selfing winter annual, has invaded a variety of habitats in western North America. Seeds are at least conditionally dormant at dispersal in early summer and lose dormancy through dry after-ripening. In the field, patterns of germination response at dispersal vary among populations and across years within populations. Degree of dormancy at summer temperatures in recently harvested seeds, as well as rate of dormancy loss during dry storage, can be related to the risk of premature summer germination in different habitats. Patterns of dormancy loss are predictable and can be modeled using hydrothermal time concepts. To assess the relative contribution of genotype and maturation environment, multiple parental lines from contrasting populations were grown for three generations under manipulated greenhouse conditions. Significant germination response differences among populations were observed, as well as major differences among full-sib families. Among-population variation accounted for over 90% of the variance in germination traits, whereas within-family variance accounted for 1% or less. Populations from predictable extreme environments (subalpine meadow and warm desert margin) showed significantly less variation among families than did populations from less predictable environments (cold desert, foothill, and plains). Environmental conditions that shortened the seed ripening period (water stress and high temperature) resulted in reduced seed dormancy level at maturation, but there were strong inbred line–environment interactions. For fully after-ripened seeds, inbred line and environmental effects were no longer evident, indicating that differences in genotype and maturation environment function mainly to regulate dormancy and dormancy loss rather than to mediate response patterns of nondormant seeds.

Nomenclature: Downy brome, *Bromus tectorum* L. BROTE.

Key words: Germination, heritability, modeling, population genetics.

Downy brome, a winter annual native to Eurasia, has invaded a wide variety of habitats in western North America within the past 100 yr (Mack 1981). Over 100 million acres (40 million ha) of predominantly sagebrush steppe wildlands are now dominated by this species, and the colonization of semiarid western habitats by downy brome has been called "the most significant plant invasion in the modern history of North America" (D'Antonio and Vitousek 1992). Whereas the initial success of downy brome was attributable to disturbances such as grazing and cultivation, its current dominance is also associated with a dramatic increase in fire frequency. For many sagebrush steppe ecosystems, the average presettlement fire cycle ranged from 60 to 110 yr, but now it is less than 5 yr (Billings 1994; Whisenant 1990).

Efforts to manage wildlands to either prevent the spread of downy brome or restore areas to native vegetation will presumably benefit from an understanding of the mechanisms that allow this weed to invade and persist. As with many weeds, issues related to the regulation of germination timing through seed dormancy are central to an understanding of downy brome biology and are the focus of this paper.

Patterns of Seed Dormancy Loss

Downy brome seeds ripen in early- to midsummer and exhibit varying degrees of dormancy at maturation (Allen et al. 1995; Beckstead et al. 1996; Milby and Johnson 1987). Populations of dormant seeds may show some germination, but such seeds germinate slowly and nonuniformly. Although slow germination has often been interpreted as an indication of low vigor (e.g., Steiner 1990), this is clearly not the case for downy brome seeds because they will eventually acquire the ability to germinate quickly and nearly completely. Seeds lose dormancy through dry after-ripening, which is characterized by progressive changes in dormancy level as well as speed and uniformity of germination (Figure 1). After-ripened seeds germinate in response to autumn rains, postpone germination until winter or early spring, or carry seeds across years as components of the soil seed bank. Expression of seed dormancy is strongly dependent on collection site and incubation temperature, with higher incubation temperatures generally associated with reduced percentage and rate of germination (Figure 2). Fully after-ripened seeds germinate rapidly and completely across a wide temperature range (Allen et al. 1995; Beckstead et al. 1996).

Ecological Relevance of Seed Dormancy

When seeds collected from contrasting populations are subjected to controlled dry storage followed by incubation across a range of temperatures, differences among production years as well as populations are evident. For example, germination of recently harvested seeds collected from three states ranged from 0 to 80%, depending on population as well as incubation temperature of the germination assay (Beckstead et al. 1996). Differences in germination per-

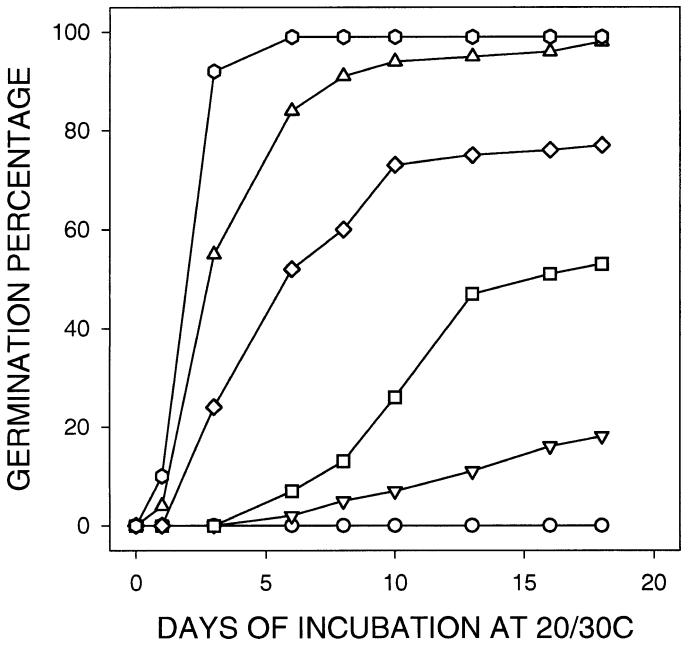

FIGURE 1. Selected cumulative time courses for germination of Green River downy brome (*Bromus tectorum* L.) seeds at 20/30 C during different stages of after-ripening. Recently harvested seeds (circles) failed to germinate. As after-ripening progressed, seeds germinated to higher percentages and eventually reached maximum rate and uniformity. (Circles, recently harvested seeds; inverted triangles, 1 mo storage at 20 C; squares, 1 mo storage at 30 C; diamonds, 3 mo storage at 20 C; triangles, 4 mo storage at 20 C; hexagons, 4 mo storage at 30 C.) Adapted from Allen et al. (1995).

centages between years ranged from almost none to more than 60%, again depending on germination assay temperature and population. Many native plant species that cooccur with downy brome show ecologically significant variation in regulation of seed germination timing (e.g., Meyer et al. 1989 for gray rabbitbrush [*Chrysothamnus nauseosus* (Pallas) Britt.]; Meyer and Monsen 1991 for big sagebrush [*Artemisia tridentata* Nutt.]; Meyer 1992 for Eaton penstemon [*Penstemon eatonii* Gray]; and Meyer and Kitchen 1994 for perennial flax [*Linum perenne* L.]). For these species, seed dormancy functions to time the germination so that environmental risks associated with seedling establishment (e.g., drought and frost) are minimized. The variation in seed dormancy is ecologically significant for native plants and has resulted in contrasting ecotypes following many generations of selection. We were interested to learn whether variation in downy brome seed dormancy was also ecologically meaningful, given the relatively recent introduction of this species into western ecosystems.

When seed dormancy responses for 21 widely differing downy brome populations were compared, distinct response syndromes characterized groups of populations (Meyer et al. 1997). For example, Mohave desert populations had the most conservative high-temperature germination response. Rainfall that is adequate to support seedling establishment may not come until December or later in these habitats, whereas seeds ripen in June or earlier. Extended hot weather interrupted by irregular heavy thunderstorms poses a risk of premature summer germination. The risk of precocious germination is substantially reduced through high primary dormancy and slow after-ripening in terms of high-temperature incubation response. In contrast, montane populations were

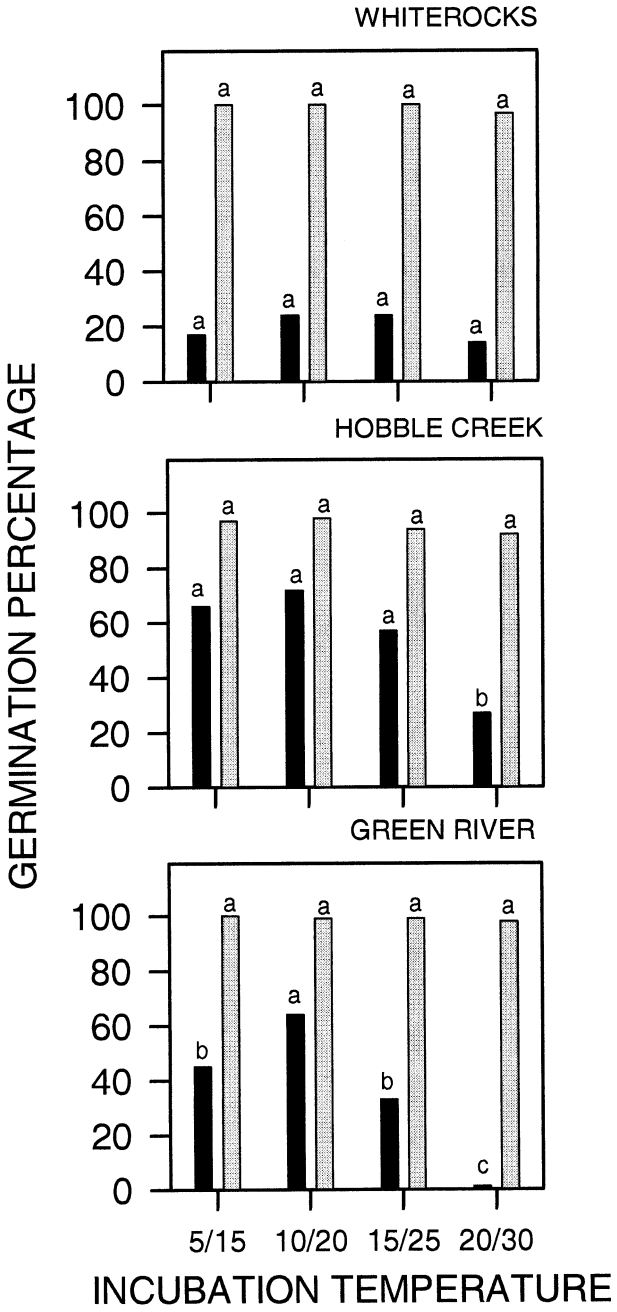

FIGURE 2. Germination percentages for recently harvested and fully after-ripened (stored 4 mo at 40 C) downy brome (*Bromus tectorum* L.) seeds of three collections following 28 d of incubation at four temperatures. All values for recently harvested seeds are significantly lower than values for fully after-ripened seeds ($P < 0.05$). For each line, values associated with the same letter are not significantly different ($P < 0.05$). Adapted from Allen et al. (1995).

the least conservative in terms of germination response. Seed maturation in these habitats is delayed until late July, and conditions are often immediately favorable for growth. As expected, collections from intermediate habitats (e.g., intermountain desert and foothill populations), where weather conditions vary widely and unpredictably, showed intermediate responses. These findings demonstrate that variation in seed dormancy is ecologically significant for downy brome, just as it is for native species that occupy the same habitats. It is interesting that these differences have developed in a relatively brief time (i.e., approximately 100 yr).

Predicting Seed Dormancy Loss

Most research dealing with the variables that influence seed germination has been conducted under controlled laboratory conditions. Whereas laboratory experiments have provided a wealth of information on the way seeds respond to various environmental conditions (e.g., temperature, light, and water), simulation modeling allows the best test of whether seed responses in the laboratory can be used to make meaningful predictions about dormancy loss and germination in the field. Our recent efforts to model seed dormancy loss for downy brome have been based on the concepts of hydrothermal time. Hydrothermal time is an extension of the more familiar thermal time (used throughout biology to describe the rate of biological processes as a function of temperature) and allows for progress toward germination under any given temperature and water potential conditions to be characterized. Hydrothermal time is an approach to modeling seed germination that was originally proposed by Gummerson (1986) but has been significantly developed by Bradford and coworkers (for reviews, see Bradford 1990, 1995, 2002). The parameters of hydrothermal time accumulation (hydrothermal time constant, fraction of viable seeds in the population, base temperature, mean base water potential, and standard deviation of base water potentials) are generally considered constant for a population of nondormant seeds, although Bradford (1995) speculated that progressive loss of dormancy in a seed population may be related to a progressive decrease in the mean base water potential (i.e., the average water potential threshold below which germination will not occur; it is assumed that variation in base water potentials within a population is normally distributed and accounts for variation among seeds in germination time requirements).

We conducted several studies to determine that dormancy loss during dry after-ripening could be modeled on the basis of decreasing mean base water potential and that hydrothermal time concepts could be used in simulation modeling to predict dormancy loss under the widely fluctuating seedbed conditions that occur in the field. Under laboratory conditions, allowing the mean base water potential to vary while holding all other parameters constant accounted for variation in germination time course curves as after-ripening progressed (Christensen et al. 1996).

Dormancy loss of downy brome seeds can also be described using a thermal after-ripening time model (Figure 3). This model is based on the observation that the rate of change in mean base water potential is a linear function of temperature above a base temperature (Bauer et al. 1998). The thermal time requirement for after-ripening is the amount of thermal time required for the mean base water potential to change from its initial value (i.e., the value for recently harvested seeds) to the final value (i.e., the value for fully after-ripened seeds). Thermal after-ripening time models are currently being extended to generalize model parameters across incubation temperatures (P. S. Allen and S. E. Meyer, unpublished data; Meyer et al. 2000).

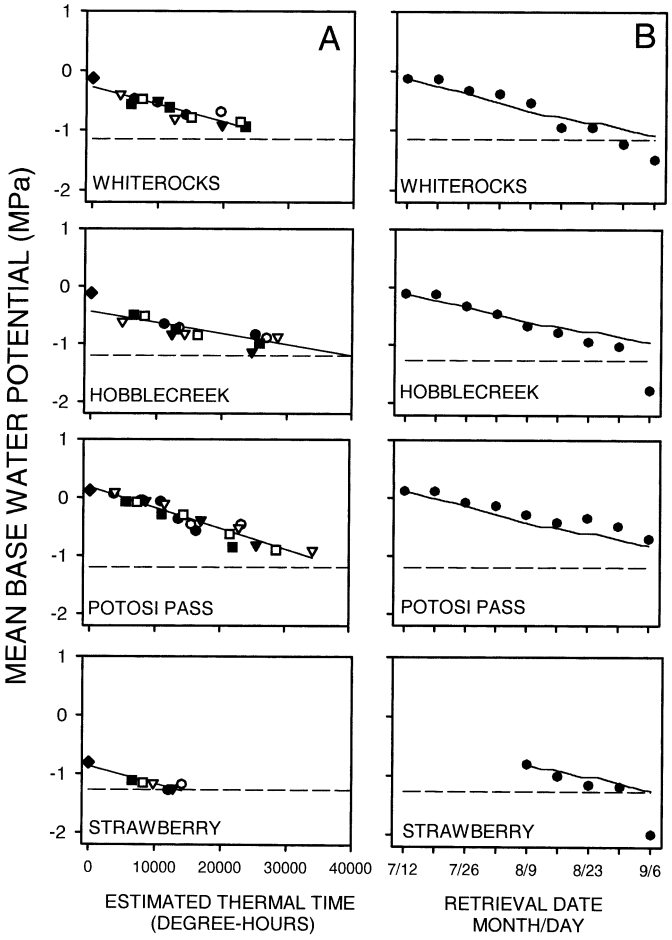

FIGURE 3. (A) Calculated values of the mean base water potential plotted against time elapsed in dry storage at a range of temperatures for seed collections from four populations of downy brome (*Bromus tectorum* L.), as measured at 10/20 C incubation temperature. (B) Calculated values of the mean base water potential for seeds retrieved from the field and incubated at 10/20 C, plotted against time elapsed under field conditions. The points represent empirical data, and the solid lines represent simulated values based on a thermal time model of after-ripening, using seed zone temperature as the driving variable. The dotted lines represent the minimum value of the mean base water potential for each seed collection at 10/20 C. Adapted from Bauer et al. (1998).

Ecological Genetics of Seed Dormancy

The genetic basis that contributes to the high invasive potential of downy brome may be attributed to preadaptations from founder populations, rapid evolution of distinct populations that show adaptive responses to their respective habitats, a generalist genotype that shows great plasticity over a wide range of environments, or a combination of the above possibilities (Bradshaw 1965).

Downy brome is an exclusively self-pollinating species with low levels of genetic variation (McKone 1985). Most of that genetic variation is concentrated between populations rather than between full-sib families within a population. Allozyme variation is also low in comparison with other diploid plants. In a greenhouse study by Rice and Mack (1991), within-family variance (assumed to be because of phenotypic plasticity) dominated the variance structure for plant size at maturity, seed number, total seed weight, and individual seed weight. Only flowering time, a trait under strong selection for survival, showed significant between-population genetic variation that was correlated with habitat. Seed germination phenology was not examined in their study, even though there is heavy selection pressure for this trait in annual plants (Angevine and Chabot 1979), and the probability of survival in the field has been strongly tied to

emergence phenology for downy brome (Mack and Pyke 1984; Pierson and Mack 1990).

To address the question of genetic vs. environmental contributions to variation in downy brome seed dormancy, we conducted a 3-yr greenhouse study (results of first two years in Meyer and Allen 1999a, 1999b). Five specific questions were addressed:

1. Are among-population differences in dormancy status at dispersal genetically based?
2. How much of the phenotypic variance in dormancy status is the result of differences among populations, differences among families within populations, and variation within families?
3. Do successive greenhouse-produced generations of inbred lines with contrasting dormancy exhibit consistent dormancy phenotypes?
4. How does maturation environment (water stress, maturation temperature, and nitrogen level) influence seed dormancy?
5. Based on results from the above questions, what are the relative contributions of genotype, maternal environment, postharvest history, and germination environment to the control of dormancy phenotype?

Details of experimental design, as contained in the original papers (Meyer and Allen 1999a, 1999b; Meyer et al. 2001), are briefly summarized here. Six widely contrasting populations of downy brome were selected based on previous work. In the first year (1993), seeds at each site were collected from 10 individual plants, and progeny grown from seeds of each field-collected plant were considered to belong to different inbred families ($n = 60$). Field-collected seeds were allowed to after-ripen before seeds were planted in the greenhouse. The greenhouse environment simulated autumn, winter, and then spring conditions. At maturation, seeds were harvested and subjected to incubation at various temperature regimes. Germination rates and percentages were recorded and analyzed; comparisons were made between responses from greenhouse-grown plants and their parents, which had been subjected to identical germination experiments the previous year. In the second year (1994), for each of the six populations, we chose the lines with maximum, minimum, and median mean germination percentages, for a total of 18 inbred lines. Plants were grown as in the previous year, except that three levels of water stress were applied during maturation. In the third year of the study (1995), maturation environment was manipulated to provide for low- vs. high–maturation temperature and low vs. high fertility. The third-year study included six inbred lines from each of two populations.

Significant differences among populations were observed after greenhouse cultivation. Among-population variation accounted for over 90% of the variance in germination rate and percentage, whereas within-family variance accounted for 1% or less. Differences among populations in seed dormancy were more pronounced at higher incubation temperatures. As in our previous ecological studies, the warm desert population (Potosi Pass) showed essentially complete dormancy (germination percentages near zero) at 20/30 C, whereas the high-elevation montane population (Strawberry) was completely nondormant. Populations from intermediate, and therefore less predictable, habitats showed much greater among-family variance in germination traits than did populations from more predictable habitats (Figure 4). For example, populations from the more extreme habitats (Potosi Pass and Strawberry) tended to have similar germination percentages among all family members, whereas populations with high among-family variance (Green River) showed germination percentages that ranged from nearly completely nondormant at most incubation temperatures to nearly completely dormant at those same temperatures.

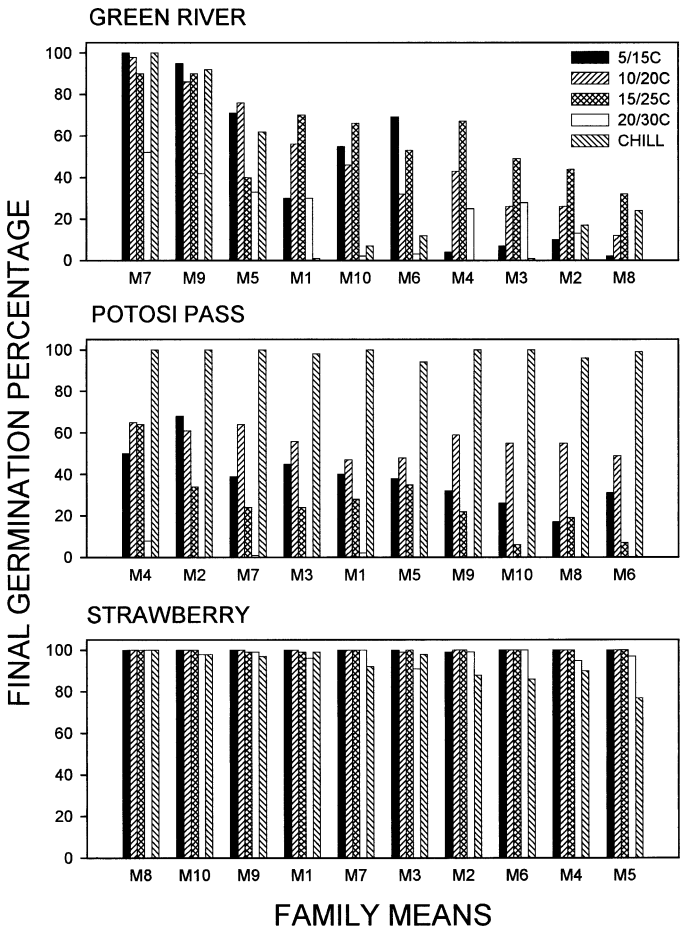

FIGURE 4. Family mean germination percentages in five incubation treatments for recently harvested seeds of ten full-sib families belonging to Green River, Potosi Pass, and Strawberry populations of downy brome (*Bromus tectorum* L.). Within a population, families are ranked by mean germination percentage across the five treatments. Adapted from Meyer and Allen (1999a).

The level of genetic control over seed dormancy can be evaluated by comparing germination responses for field-collected seeds with those of greenhouse-grown progeny. When mean germination percentages for greenhouse populations were regressed on means obtained from wild-collected seeds, the relationship was positive and significant, although there was a slight decrease in dormancy (increased germination percentages) in the greenhouse relative to wild collections (Meyer and Allen 1999a). A similar regression of mean germination percentages for generations one and two was even more dramatic (Figure 5), showing that successive greenhouse-produced generations of inbred lines indeed exhibit consistent dormancy phenotypes. Regressions at intermediate temperatures (10/20 C and 15/25 C) did not differ from the 1:1 line expected if seeds from each generation had the

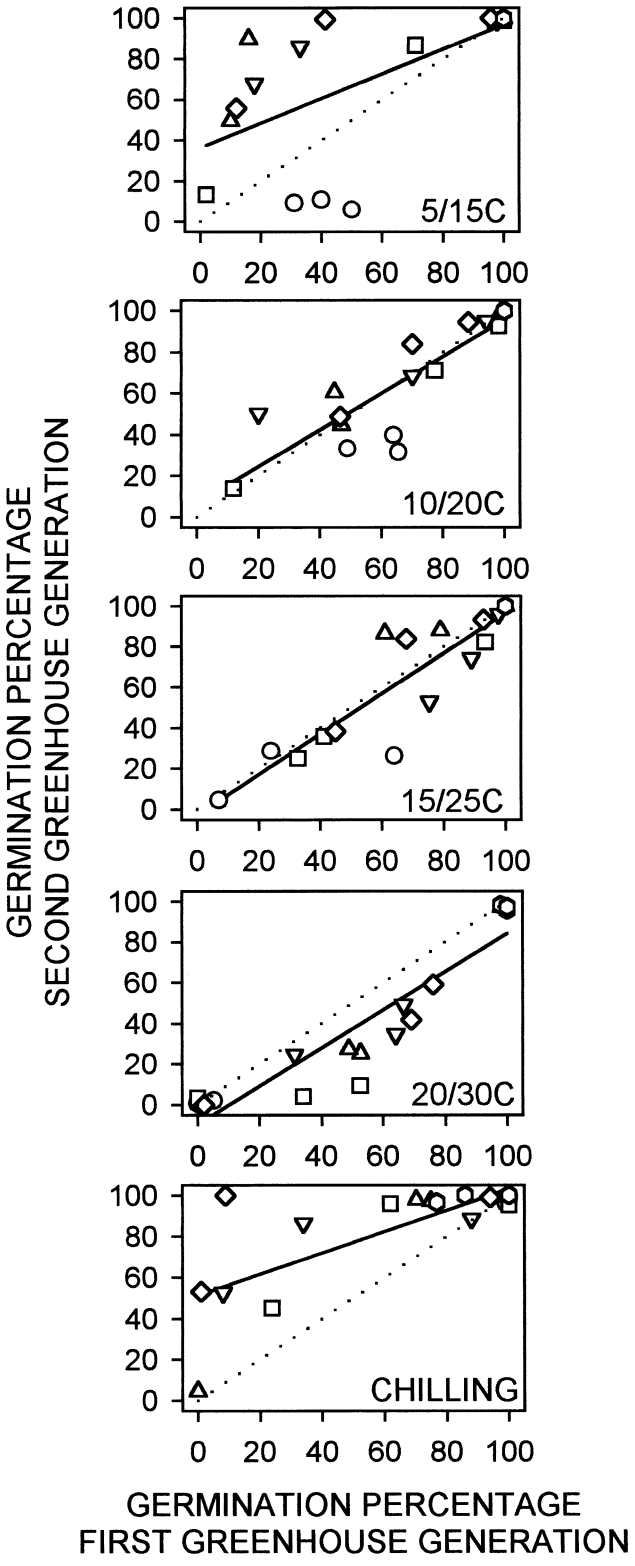

FIGURE 5. Germination percentages for recently harvested downy brome (*Bromus tectorum* L.) seeds of second-generation greenhouse-grown plants belonging to 18 inbred lines from six populations, regressed on germination percentages for recently harvested seeds of their greenhouse-grown parents. Solid lines are regression lines; dotted lines represent a 1:1 relationship. Regression equation for 5/15 C: $y = 0.608x + 36.3$, $R^2 = 0.399$, $P < 0.01$; for 10/20 C: $y = 0.892x + 6.54$, $R^2 = 0.763$, $P < 0.0001$; for 15/25 C: $y = 0.993x - 2.55$, $R^2 = 0.819$, $P < 0.0001$; for 20/30 C: $y = 0.936x - 9.53$, $R^2 = 0.863$, $P < 0.0001$; for chilling (1 C for 10 wk followed by incubation at 10/20 C for 4 wk): $y = 0.518x + 51.4$, $R^2 = 0.561$, $P < 0.001$. (Circles, Potosi Pass; squares, Green River; triangles, Whiterocks; inverted triangles, Hobble Creek; diamonds, Castle Rock; hexagons, Strawberry.) Adapted from Meyer and Allen (1999b).

same values. Regressions at other incubation temperatures were also significant, even though the regression for 20/30 C incubation had a *y*-intercept that was offset slightly downward. At the lower temperatures, there was again a slight decrease in dormancy from seeds produced during the second greenhouse generation. These slopes represent a measure of heritability for seed dormancy, which in this case is very high. The high degree of heritability further indicates that among-population and among-line phenotypic differences observed in the first greenhouse generation were indeed genetically based and were not a consequence of among-habitat differences in the maternal environment of the wild-collected progenitors. Significant heritability for seed dormancy has been demonstrated for a number of other wild plant species (e.g., Garbutt and Witcombe 1986; Lane and Lawrence 1995; Platenkamp and Shaw 1993).

Although the genetic component of seed dormancy in downy brome is clear, maturation environment can also mediate the expression of seed dormancy (Meyer and Allen 1999b). For example, seeds that experienced high maturation water stress were generally less dormant than those experiencing medium or no water stress. Averaged across populations, germination percentages for seeds that experienced high water stress were 76%, compared to 66% for both medium and no water stress. As expected, inbred lines with low dormancy (i.e., those with a high germination percentage) were generally the least affected by maturation water stress. High maturation temperature also led to reduced seed dormancy, especially as expressed at low incubation temperatures (Figure 6). Although fertility effects were statistically significant, they were inconsistent and generally negligible.

Conclusions

Genotype, maternal environment, postharvest history, and germination environment, all contribute to the control of dormancy phenotype and seed germination in downy brome. Dormancy in seed collections from extreme habitats is almost entirely under genetic control, as environmental conditions during maturation have little effect on germination of recently harvested seeds. In contrast, inbred lines that vary in degree of seed dormancy characterize populations from intermediate habitats. Dormancy status for many of these lines varies significantly with maturation water stress and temperature, as well as with germination environment. In general, environmental conditions that lead to shortened seed ripening periods result in reduced seed dormancy, as if the block to germination is able to accumulate to a greater degree if seed maturation is prolonged.

Differences in seed dormancy that are evident in recently harvested seeds largely disappear during after-ripening. Collections of nondormant seeds germinate rapidly and completely, regardless of genotype or environmental factors likely to be encountered. This suggests that seed dormancy in downy brome functions largely to regulate germination timing primarily during the summer and autumn of maturation. Particularly for intermediate populations, where several genotypes coexist, variation in summer and autumn weather

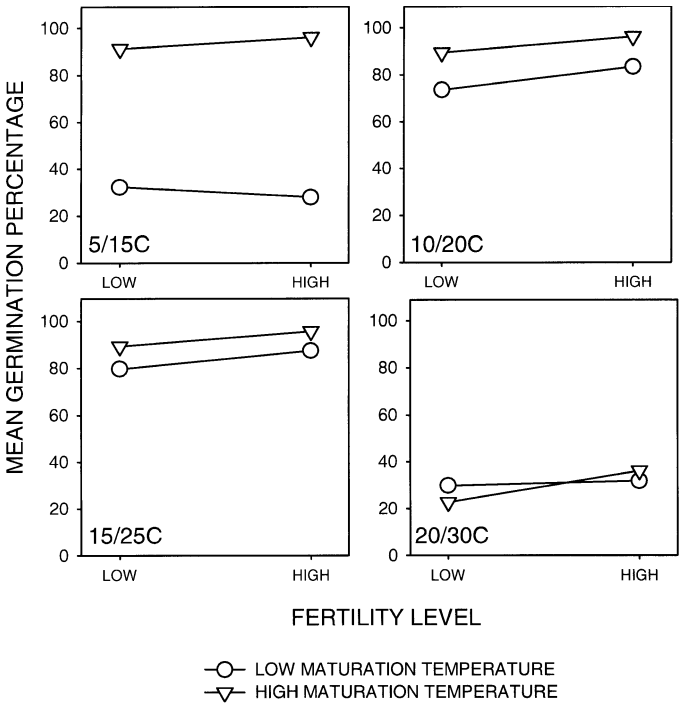

FIGURE 6. Mean germination percentages for recently harvested seeds belonging to 12 inbred lines of downy brome (*Bromus tectorum* L.) (six lines each from the Whiterocks and Hobble Creek populations) grown in the greenhouse under a factorial combination of low- vs. high–maturation temperature (21:16 C day–night vs. 30:18 C day–night) and low- vs. high–soil fertility regime (20:20:20 fertilizer at 100 μg mg^{-1} vs. 1,000 μg mg^{-1}). *F*-values from analysis of variance: maturation temperature, $F = 614.2$, df = 1, $P < 0.0001$; fertility, $F = 37.4$, df = 1, $P < 0.0001$; incubation temperature, $F = 671.5$, df = 1, $P < 0.0001$; fertility × maturation temperature, $F = 8.0$, df = 1, $P < 0.0001$; fertility × incubation temperature, $F = 3.8$, df = 1, $P < 0.02$; maturation temperature × incubation temperature, $F = 214.7$, df = 1, $P < 0.0001$; fertility × maturation temperature × incubation temperature, $F = 2.6$, $P < 0.06$.

patterns can lead to altered frequencies of a particular genotype at a particular location. Based on the obligate self-pollinating behavior of downy brome, there are two possibilities to explain the genetic variability for seed dormancy in light of the relatively recent introduction of downy brome into western North America. Founder populations could have contained multiple lines, or multiple source populations containing unique dormancy genotypes could have been introduced. Characterization of downy brome at the molecular level (Meyer et al. 2001; Ramakrishnan et al. 2002) suggests that at least some populations are so distinct that they likely resulted from separate introductions.

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